The Holocene treeline in the northern Andes (Ecuador): First evidence from soil charcoal

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Abstract

Indications for the speed and timing of past altitudinal treeline shifts are often contradictory. Partly, this may be due to interpretation difficulties of pollen records, which are generally regional rather than local proxies. We used pedoanthracology, the identification and dating of macroscopic soil charcoal, to study vegetation history around the treeline in the northern Ecuadorian Andes. Pedoanthracology offers a complementary method to pollen-based vegetation reconstructions by providing records with high spatial detail on a local scale. The modern vegetation is tussock grass páramo (tropical alpine vegetation) and upper montane cloud forest, and the treeline is located at ca. 3600 m. Charcoal was collected from soils in the páramo (at 3890 and 3810 m) and in the forest (at 3540 m), and represents a sequence for the entire Holocene.

The presence of páramo taxa throughout all three soil profiles, especially in combination with the absence of forest taxa, shows that the treeline in the study area has moved up to its present position only late in the Holocene (after ca. 5850 cal years BP). The treeline may have been situated between 3600 m and 3800 m at some time after ca. 4900 cal years BP, or it may never have been higher than it is today. The presence of charcoal throughout the profiles also shows that fires have occurred in this area at least since the beginning of the Holocene.

These results contradict interpretations of palaeological data from Colombia, which suggest a rapid treeline rise at the Pleistocene–Holocene transition. They also contradict the hypothesis that man-made fires have destroyed large extents of forest above the modern treeline. Instead, páramo fires have probably contributed to the slowness of treeline rise during the Holocene.

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1. Introduction

The present position of alpine treelines is to a large extent the result of historical ecological processes, influenced by past climates and land use. Knowing the vegetation history is therefore essential for understanding treeline positions. The present position of tropical treelines is thought to be lower than their potential position, yet it is unknown what this potential position is, due to a lack of both ecological and historical information about tropical treeline ecosystems.

According to some authors, the potential treeline altitude is indicated by the uppermost forest patches
found above the actual treeline. These are interpreted as remnants of high altitude forests now destroyed by man-made fires and forest clearing (Ellenberg, 1958; Laegaard, 1992; Sarmiento and Frolich, 2002). However, there is no evidence that these highest patches have ever been surrounded by forests (Islebe and Hooghiemstra, 1997; Wille et al., 2002), and present patches are mostly restricted to special microsites such as ravines and boulder slopes (Troll, 1959; Walter and Medina, 1969). The situation for forest patches at lower altitudes, close to the actual treeline, is less clear. These may also rely on locally favorable conditions, or may be remnants of formerly more extensive forests (Miehe and Miehe, 1994; Kessler, 2002).

In the northern Andes, the alpine vegetation above the treeline is called ‘páramo’ (Monasterio, 1980; Balslev and Luteyn, 1992; Hofstede et al., 2003). The most common type of páramo in Ecuador is tussock grass páramo, dominated by large tussock grasses interspersed with various shrubs and herbs (Ramsay and Oxley, 1997; Mena Vásconez and Medina, 2001). Classifications of the páramos of Colombia distinguish three altitudinal zones: a subpáramo, dominated by shrubs; a ‘páramo proper,’ dominated by tussock grasses; and a sparsely vegetated superpáramo (Cuatrecasas, 1958; Van Der Hammen and Cleef, 1986). In Ecuador, however, the shrubby subpáramo zone is usually absent (Mena Vásconez and Medina, 2001). Most páramos in Ecuador are burned regularly, especially where they are used for livestock grazing (Laegaard, 1992). These fires may have increased the dominance of tussock grasses at the expense of shrubs, especially in the lower parts of the páramo (Van Der Hammen and Cleef, 1986; Ramsay and Oxley, 1997; Suarez and Medina, 2001).

Below the treeline we find upper montane forest, comprising several forest types, including dwarf forests (Cleef and Hooghiemstra, 1984). Some synonyms or subclassifications of these forests are sub-alpine rain forest, andean cloud forest, elfin forest, mossy forest, dwarf cloud forest, ‘bosque alto-andino’ or ‘ceja andina’ (see e.g. Webster, 1995; Jørgensen et al., 1999). These forests are characterized by low stature trees with small sclerophyllous leaves, and abundant moss cover on both the trees and the forest floor. They are species-poor compared to tropical rain forests at lower altitudes (Gentry, 1995), but very species-rich compared to upper montane forests in temperate regions. Common tree genera are Weimannia, Ilex, Ocotea, Oreopanax, Hedysosmum, Clusia, Clethra, Miconia, Podocarpus, Rapanaea, Brunellia, Hesperomeles, Giaiadendron, Polylepis, Escallonia, Gynoxys etc. (Cleef and Hooghiemstra, 1984; Van Der Hammen and Cleef, 1986; Gentry, 1995).

The Holocene history of treeline dynamics in the northern Andes has been addressed by an increasing number of palynological studies since the 1960s (e.g. Van Der Hammen and Gonzalez, 1960; Van Geel and Van Der Hammen, 1973; Hooghiemstra, 1984; Colinvaux et al., 1997; Hansen et al., 2003). There is, however, no general consensus about what happened in the different periods of the Holocene, as pollen data or their interpretations are frequently contradictory, and the timing of events is rather uncertain (Markgraf, 1989; Van’t Veer et al., 2000; Marchant et al., 2001).

In the late Pleistocene, several warm and colder periods occurred between the end of the last glacial and the early Holocene (Van Der Hammen and Cleef, 1986). In the last cold period, a Younger Dryas equivalent (sensu Van Der Hammen and Hooghiemstra, 1995) referred to as the ‘El Abra stadial’ (ca. 11,000 to 9500 14C years BP), treelines were strongly lowered, down to altitudes 600–800 m lower than today (Van Der Hammen and Hooghiemstra, 1995). After this cold and arid period treelines are thought to have risen rapidly in response to the climatic warming in the early Holocene (Van Geel and Van Der Hammen, 1973; Van Der Hammen, 1974; Flenley, 1979; Bush et al., 2005), though other studies show a later rise due to the continuation of arid conditions until ca. 8500 14C years BP (Islebe and Hooghiemstra, 1997; Van’t Veer et al., 2000; Berrio et al., 2002).

In the middle Holocene, between ca. 7000 and 5000 14C years BP, the climate is thought to have been warmer (‘hypothermal’), as shown by high treeline altitudes (Van Der Hammen, 1974; Van Der Hammen and Cleef, 1986) and δ18O data (Thompson et al., 1995). However, other studies find indications for a drier climate, resulting in lowered treelines (Hansen and Rodbell, 1995; Marchant et al., 2001; Berrio et al., 2002; Marchant et al., 2002a; Vélez et al., 2003). Records for this period are particularly heterogeneous (Marchant et al., 2001).

For the late Holocene, studies show an increase in humid forest taxa between 4000 and 3000 14C years BP, indicating a return to more humid conditions (Marchant et al., 2001, 2002a; Hansen et al., 2003). Meanwhile the appearance of crop and disturbance taxa suggests the beginnings of regional agriculture and possible forest clearance (Hansen and Rodbell, 1995; Wille et al., 2002; Hansen et al., 2003; Vélez et al., 2003). A lowering of treelines after 3000 14C years BP is generally interpreted as an effect of human disturbance, masking the climatic signal (Hansen and Rodbell, 1995; Wille et al., 2002; Vélez et al., 2003; Bush et al., 2005).

Although pollen records provide valuable information about past vegetation cover, pollen-based reconstructions
of treeline shifts are rarely spatially precise, because pollen can be transported long distances by wind. Also, pollen records hardly ever allow for an unambiguous interpretation, because the pollen signal depends not only on vegetation distribution, but also on other variable factors like wind direction (Hansen et al., 2003) and lake size (Markgraf, 1989). This may partly explain the contradictory results of different palynological studies in the Andes, although regional differences in climate and vegetation history are probably also important.

The usual method for reconstructing the fire history of the vegetation is counting charcoal particles on pollen slides (Patterson et al., 1987; Clark, 1988; Haberle and Ledru, 2001). However, unlike pollen, this microscopic charcoal is easily transported by wind (Clark, 1988) and the palaeofire can therefore not be precisely located. Another disadvantage is that the type of vegetation burned is derived indirectly, from the pollen spectrum. A more local signal of past fires and vegetation cover is offered by macroscopic charcoal fragments in the soil.

Soil charcoal analysis (pedoanthracology) was first developed in France (Thinon, 1978), and is based on anatomical identification and $^{14}$C dating of charcoal fragments (≥0.4 mm) from the soil. Charcoal is composed of inorganic carbon and therefore does not decompose in the soil. In contrast to pollen, charcoal is conserved in all types of soil. Botanical identification of charcoal fragments is possible because the wood structure is conserved during carbonization. The charcoal fragments are not very mobile, because of their relatively large size (Clark et al., 1998; Ohlson and Tryterud, 2000), and provide a proxy for the local species composition with high spatial precision.

In spite of these advantages, pedoanthracology is still not widely applied. Most pedoanthracological studies have been carried out in the French Alps to reconstruct altitudinal changes in treeline location (Carcaill and Thinon, 1996; Talon et al., 1998). In these studies evidence could be found for the presence of forest above the actual treeline (Carcaill and Brun, 2000), but the presence of alpine vegetation, and hence the absence of forest, was impossible to infer from the data, because the alpine meadows contain few or no woody species and leave no charcoal. In contrast, in the tropics the vegetation above treeline contains various woody species whose presence in the charcoal record can indicate the absence of forest. The only pedoanthracological studies in the tropics so far have been located in lowland areas in Brazil (Scheel-Ybert et al., 2003) and French Guyana (Tardy, 1998). Ours is the first pedoanthracological study in tropical mountains.

In this paper we show how macroscopic charcoal from the soil allowed the reconstruction of vegetation cover and treeline position since the late Pleistocene in northern Ecuador. Our objective was to verify whether the treeline has been higher in the past, and what has been the role of fire in its dynamics. We compare our results with those from several palynological studies in the northern Andes and present our view on the dynamics of tropical alpine treelines. In order to be able to identify the historical soil charcoal, we have also created the first reference database of wood anatomy for tropical Andean species.

2. Study area

The study area is situated on the western flanks of the eastern Cordillera in northern Ecuador at the treeline in the protected area of Guandera Biological Station (0° 36’ 00” N, 77° 41’ 35” W, Fig. 1). The station conserves one of the last extensive upper montane cloud forests on the inner slopes of the Ecuadorian Andes, and the best conserved stand of montane Clusia forest known in Ecuador (H. Navarrete, Universidad Católica Quito, pers. comm. 2005). The cloud forest occurs between the agricultural area (mainly potato cultivation) below and the páramo above.

The area has a typical humid tropical alpine climate with low temperatures and high precipitation all year round, and strong diurnal, but weak annual temperature fluctuations. Climate data from a forest clearing at 3370 m asl (above sea level), ca. 2 km from our transect, indicate an annual precipitation sum of ca. 1700 mm for 2002, and daily temperatures at between 4 °C and 19 °C in most months (average not recorded) (Bader et al., 2007a). One-week measurements in the páramo showed temperatures between 2 °C and 19 °C at 1.50 m (Bader et al., 2007b). The soil of the páramo is a deep and well developed Andosol (Soil Survey Staff, 1999). The soil of the forest has an organic upper horizon of 30–100 cm consisting principally of roots.

The upper montane cloud forest at the treeline has a mixed canopy composed mainly of the tree species Ilex colombiana Cuatrec. (Aquifoliaceae), Weinmannia cochensis Hieron. (Cunoniaceae), Miconia tinifolia Naudin (Melastomataceae), Clusia flaviflora Engl. (Clusiaceae) and Gaiadendron punctatum (Ruiz & Pavón) G. Don. (Loranthaceae). The most common shrub species in the forest understory are various Ericaceae, Miconia chlorocarpa Cogn. (Melastomataceae), and Desfontainia spinosa Ruiz & Pav. (Loganiaceae). At the forest edge large Diplodestephium shrubs (Asteraceae) and caulescent Blechnum ferns (Blechnaceae) are the most common elements. Down from ca. 100 m below the treeline, stands of Clusia-dominated forest are found. The treeline is an abrupt boundary between forest and tussock grass.
páramo. It is located at ca. 3600 m asl, and judging from historical aerial photographs it has been at this position for at least 40 years. Up to ca. 100 m from the treeline, in topographical depressions and valleys, there are several small patches of forest with the same species composition as the continuous mixed forest (Fig. 2).

The páramo vegetation consists mostly of large tussock grasses (*Festuca* sp., *Calamagrostis* sp.) interspersed with the terrestrial Bromeliad *Puya hamata* L.B. Smith, with the tall (up to 4 m) stem rosette *Espeletia pycnophylla* Cuatrec. (Asteraceae), and with small shrubs like *Pernettya prostrata* (Cav.) DC. (Ericaceae), *Pentacalia*
vaccinoides (Kunth) Cuatrec. (Asteraceae), Brachyotum alpinum Cogn. (Melastomataceae) and Hypericum lar-icifolium Kunth. (Clusiaceae). Only three forest tree species were found regenerating in the páramo: seedlings and saplings of Weinmannia cochensis and Diplostephium sp., and clonal shoots of Gaiadendron punctatum were abundant close to the treeline, but no adult plants of these species were found in the páramo (Bader et al., 2007a).

At the present time, the páramo vegetation is burned approximately every 3–6 years. There are no records of naturally induced fires. In other regions fire is often used as a pasture management tool, but in Guandera there are no indications of present or past livestock grazing. Here, the main reason for burning the páramo is the local belief that these fires will induce rainfall. The páramo dries rapidly under the strong solar radiation and it then burns well because of the abundance of dead plant material in the tussocks. In contrast, the cloud forest maintains a moist microclimate because of the abundance of mosses, and it is not affected by fire except sometimes at the very edges, where trees may get scorched (pers. obs.). After a fire the páramo vegetation, especially the tussock grass, recovers rapidly. In contrast, shrubs and any small trees that may have appeared in the páramo (always of the

Fig. 2. Photo of the lower part of the study area. In the foreground and on the right tussock grass páramo, on the left upper montane cloud forest. Two patches of forest can be seen in the páramo.

Fig. 3. Location of the sampling points along an altitudinal transect in Guandera Biological Station.
Table 1
Woody species in the present vegetation (upper montane cloud forest and tussock grass páramo) of Guandera Biological Station, collected for the charcoal reference collection

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Forest</th>
<th>Páramo</th>
<th>Abundance</th>
<th>Growth form</th>
<th>Veg type&lt;sup&gt;d&lt;/sup&gt;</th>
<th>Veg type&lt;sup&gt;e&lt;/sup&gt;</th>
<th>Veg type&lt;sup&gt;f&lt;/sup&gt;</th>
<th>Ecology of the species/genus according to Marchant et al. (2002b)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ilex colombiana</em> Cuatrec.</td>
<td>Aquifoliaceae</td>
<td>X</td>
<td>++</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f</td>
<td>f</td>
<td>Species: tree, up to 3600 m in Colombia, particularly in humid sites</td>
</tr>
<tr>
<td><em>Clusia flaviflora</em> Engl. and</td>
<td>Clusiaceae</td>
<td>X</td>
<td>++</td>
<td>Tr</td>
<td>F</td>
<td>f</td>
<td>f</td>
<td>f</td>
<td>Genus: trees and shrubs, wide distribution in forests up to 3200 m</td>
</tr>
<tr>
<td><em>Clusia multiflora</em> Kunth</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><em>Miconia chlorocarpa</em> Cogn.</td>
<td>Melastomataceae</td>
<td>X</td>
<td>++</td>
<td>Sh</td>
<td>d,s</td>
<td>f</td>
<td>f,d,s</td>
<td>f</td>
<td>Genus: dwarf shrubs and small trees, in moist and wet early successional forest up to 4800 m, frequent in páramo-forest transition and sub-Andean forest.</td>
</tr>
<tr>
<td><em>Miconia tinifolia</em> Naudin</td>
<td>Melastomataceae</td>
<td>X</td>
<td>++</td>
<td>Tr</td>
<td>d,s</td>
<td>f</td>
<td>f,d,s</td>
<td>f</td>
<td></td>
</tr>
<tr>
<td>Gaiadendron punctatum</td>
<td>Loranthaceae</td>
<td>X</td>
<td>X&lt;sup&gt;a&lt;/sup&gt;</td>
<td>++</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>d</td>
<td>Species: parasitic tree, common in forest-páramo ecotone, subalpine dwarf forest and shrub páramo</td>
</tr>
<tr>
<td>(Ruiz &amp; Pavón) G.Don.</td>
<td></td>
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</tr>
<tr>
<td>Weinmannia coehensis Hieron.</td>
<td>Cunoniaceae</td>
<td>X</td>
<td>X&lt;sup&gt;a&lt;/sup&gt;</td>
<td>++</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f</td>
<td>Genus: trees, common in Andean forests</td>
</tr>
<tr>
<td>Weinmannia pinnata L.</td>
<td>Cunoniaceae</td>
<td>X</td>
<td>+</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f</td>
<td>f</td>
<td></td>
</tr>
<tr>
<td><em>Oreopanax confusus</em> Marschal.</td>
<td>Araliaceae</td>
<td>X</td>
<td>+</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f,d</td>
<td>f</td>
<td>Genus: hairy trees and shrubs common in Andean forests, especially in secondary forests and from 3500 to 3700 m</td>
</tr>
<tr>
<td>Desfontainia spinosa Ruiz &amp; Pav.</td>
<td>Loganiaceae</td>
<td>X</td>
<td>+</td>
<td>Sh</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Species: small tree, present in upper Andean humid dwarf forest (3200–3500), most common genus in upper montane rainforest</td>
</tr>
<tr>
<td>Myrsine dependens (Ruiz &amp; Pav.)</td>
<td>Myrsinaceae</td>
<td>X</td>
<td>+</td>
<td>Tr</td>
<td></td>
<td></td>
<td></td>
<td>f</td>
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<tr>
<td>Spreng.</td>
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</tr>
<tr>
<td><em>Escallonia myrtilloides</em> L.F.</td>
<td>Escalloniaceae</td>
<td>X</td>
<td>+</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f</td>
<td>f</td>
<td>Species: tree, in páramo, dominant at 3000–3400 m, esp. at wet upper forest line, forms high altitude forests (3800–4100)</td>
</tr>
<tr>
<td>Macleania colocoboides A.C. Sm.</td>
<td>Ericaceae</td>
<td>X</td>
<td>+</td>
<td>Sh</td>
<td>f,s</td>
<td></td>
<td></td>
<td></td>
<td>Genus: trees and shrubs, lowland to upper montane rainforests</td>
</tr>
<tr>
<td><em>Ocotea infaroveolata</em> van der Werff</td>
<td></td>
<td>X</td>
<td>+</td>
<td>Tr</td>
<td></td>
<td></td>
<td></td>
<td>f</td>
<td></td>
</tr>
<tr>
<td>Gaultheria sclerophyllia* Cuatrec.</td>
<td>Ericaceae</td>
<td>X</td>
<td>–</td>
<td>Sh</td>
<td>s,d</td>
<td></td>
<td></td>
<td></td>
<td>Genus: shrubs, pioneer in montane areas, in forest (2800–3200 m), extending to subpáramo and páramo</td>
</tr>
<tr>
<td>Symplocos sp.</td>
<td>Symplocaceae</td>
<td>X</td>
<td>–</td>
<td>Tr</td>
<td></td>
<td>f</td>
<td>d</td>
<td></td>
<td>Genus: trees and shrubs, in mature Andean forests and about the forest line, including shrub-páramo</td>
</tr>
<tr>
<td><em>Freziera microphylla</em> Sandwith</td>
<td>Theaceae</td>
<td>X</td>
<td>–</td>
<td>Tr</td>
<td></td>
<td>F</td>
<td>f</td>
<td>f</td>
<td>Genus: trees of secondary forest/light gaps, usually found in mesic montane rainforest</td>
</tr>
<tr>
<td>Brunellia pauciflora* Cuatrec.</td>
<td>Brunelliaceae</td>
<td>X</td>
<td>–</td>
<td>Tr</td>
<td></td>
<td>F</td>
<td>f</td>
<td>f</td>
<td></td>
</tr>
<tr>
<td><strong>Clethra ovalifolia</strong> Turcz.</td>
<td>Clethraceae</td>
<td>X</td>
<td>–</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>d</td>
<td>Genus: trees and shrubs, montane forest (2800–3300 m in Colombia), 3250–3500 m in Costa Rica, extending to páramo</td>
<td></td>
</tr>
<tr>
<td><strong>Weinmannia dzieduszyckii</strong> Szyszyl.</td>
<td>Cunoniaceae</td>
<td>X</td>
<td>–</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f</td>
<td>Genus: trees, common in Andean forests</td>
<td></td>
</tr>
<tr>
<td><strong>Weinmannia auriculiformis</strong> Hieron.</td>
<td>Cunoniaceae</td>
<td>X</td>
<td>–</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f</td>
<td>Genus: trees, common in Andean forests</td>
<td></td>
</tr>
<tr>
<td><strong>Weinmannia rolloii</strong> Killip</td>
<td>Cunoniaceae</td>
<td>X</td>
<td>–</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f</td>
<td>Genus: trees, common in Andean forests</td>
<td></td>
</tr>
<tr>
<td><strong>Tristerix longibracteatus</strong> (Desr.) Barlow &amp; Wiens</td>
<td>Loranthaceae</td>
<td>X</td>
<td>–</td>
<td>Ep</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Hesperomeles obtusifolia</strong> (Pers.) Lindl.</td>
<td>Rosaceae</td>
<td>X</td>
<td>–</td>
<td>Tr</td>
<td>f,d</td>
<td>f</td>
<td>f</td>
<td>Genus: trees and shrubs prominent about Colombian upper forest line, monospecific stands in sub-Andean rain forest</td>
<td></td>
</tr>
<tr>
<td><strong>Blechnum</strong> sp.</td>
<td>Blechnaceae</td>
<td>X</td>
<td>X</td>
<td>+</td>
<td>Ca</td>
<td>d,s</td>
<td>f,d,s</td>
<td>Genus: mostly herbaceous ferns, occasionally trees, in lower páramo and sub-Andean and Andean forests (1500–3200 m)</td>
<td></td>
</tr>
<tr>
<td><strong>Thibaudia parvisilula</strong> (Benth.) Hoerold</td>
<td>Ericaceae</td>
<td>X</td>
<td>X</td>
<td>–</td>
<td>Sh</td>
<td>–</td>
<td>–</td>
<td>Genus: stem rosette growth form found from Venezuela to Ecuador, exclusive in páramo and subpáramo (3000–4400 m)</td>
<td></td>
</tr>
<tr>
<td><strong>Diplostephium spp.</strong></td>
<td>Asteraceae</td>
<td>X</td>
<td>X&lt;sup&gt;a&lt;/sup&gt;</td>
<td>+</td>
<td>Sh</td>
<td>S</td>
<td>f,s,p</td>
<td>Genus: shrubs and dwarf shrubs in high Andes. Common in grasspáramo and some forest-types from 2800–4150 m. Heliophytic&lt;sup&gt;eff&lt;/sup&gt; Species: common in páramo at ca. 3500 m</td>
<td></td>
</tr>
<tr>
<td>* <strong>Espeletia pycnophylla</strong> Cuatrec.</td>
<td>Asteraceae</td>
<td>X</td>
<td>+</td>
<td>Ca</td>
<td>p</td>
<td>p</td>
<td>–</td>
<td>Genus: heliophytic&lt;sup&gt;eff&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td><strong>Hypericum laricifolium</strong> Juss.</td>
<td>Clusiaceae</td>
<td>X</td>
<td>X</td>
<td>+</td>
<td>Ca</td>
<td>d,s,p</td>
<td>f,d,s,p</td>
<td>Genus: dominant Puna genus, but also montane rainforest plant. Species: typical in tussock grass páramo&lt;sup&gt;eff&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td><strong>Brachyotum alpinum</strong> Cogn.</td>
<td>Melastomataceae</td>
<td>X</td>
<td>+</td>
<td>Sh</td>
<td>d,s</td>
<td>f,p</td>
<td>–</td>
<td>Species: common in páramo at ca. 3500 m</td>
<td></td>
</tr>
<tr>
<td>* <strong>Pentacalia vaccinioides</strong> (Kunth) Cuatrec.</td>
<td>Asteraceae</td>
<td>X</td>
<td>+</td>
<td>Sh</td>
<td>d</td>
<td>d,p</td>
<td>–</td>
<td>Genus: heliophytic&lt;sup&gt;eff&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>* <strong>Pernettya prostrata</strong> (Cav.) DC.</td>
<td>Ericaceae</td>
<td>X</td>
<td>+</td>
<td>Sh</td>
<td>p</td>
<td>s,p&lt;sup&gt;g&lt;/sup&gt;</td>
<td>–</td>
<td>Genus: dominant Puna genus, but also montane rainforest plant. Species: typical in tussock grass páramo&lt;sup&gt;eff&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td><strong>Disterigma alaternoides</strong> (Kuth) Nied.</td>
<td>Ericaceae</td>
<td>X</td>
<td>–</td>
<td>Sh</td>
<td>s</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

Species marked with * are our indicator species. The columns ‘Forest’ and ‘Páramo’ indicate whether species occur in the forest and/or in the páramo in our study area, and column ‘Abundance’ indicates their abundance in the upper 100 m of the forest (3500–3600 m asl). These data are a summary of our vegetation transects in the forest and in the páramo (unpublished data), and for forest species we also used a floristic inventory of four 50 x 50 m forest plots in our study area (Mora, 1998). The columns ‘Veg type’ shows the occurrence of the genus in different types of vegetation, according to summaries of survey data in other parts of the Andes (see table footnotes).

<sup>a</sup> Only young regeneration in the páramo, no adult plants.

<sup>b</sup> Abundance in the upper 100 altitudinal m of the forest in Guandera: ++ = very abundant, + = common, − = rare.

<sup>c</sup> Growth form of the species: Tr = tree, Sh = shrub, Ca = caulescent rosette, Ep = epiphyte.

<sup>d</sup> Occurrence of the genus in different vegetation types: p = páramo, s = subpáramo dwarf shrub, d = subpáramo dwarf forest, f = forest. Based on vegetation classifications from Colombia (Kuhry, 1988).

<sup>e</sup> Occurrence of the genus in important quantity in forests, based on data from all along the Andes (Gentry, 1995).

<sup>f</sup> Occurrence of the genus in different vegetation types: p = páramo, s = subpáramo dwarf shrub, d = subpáramo dwarf forest, f = forest (including some dwarf forest types). Based on vegetation classifications from Colombia (Cleef and Hooghiemstra, 1984).

* *E. prostrata* is a tussock grass páramo element at species level.
species *W. cochensis*, *G. punctatum*, and *Diplostephium* sp.) die or recover much more slowly (pers. obs.).

3. Methodology

3.1. Soil sampling

Three pits were dug in an altitudinal transect: in the páramo at 3890 m asl (GUA1) and at 3810 m asl (GUA2), and in a *Clusia*-dominated part of the forest at 3540 m asl (GUA3) (Fig. 3). In the selection of pit locations we avoided steep slopes and areas with signs of past disturbances or erosional features (Carcaillet and Thinon, 1996). Pits were ca. 1 m wide, 2 m long, and 1.25 to 2 m deep. The depth was determined by the depth of a 2–3 cm impermeable layer consisting of iron oxides, below which there was a horizon of volcanic ash and pumice. The soil horizons and their colours and structure were concisely described in the field (Soil Survey Staff, 1999). The actual vegetation was described around each sampling point, in plots of 5 × 5 m in the páramo and 20 × 20 m in the forest, estimating ground cover and height of the different vegetation layers and species.

Samples were taken from the base of the pit first and then upwards in levels of ca. 25 cm thickness. The levels did not cross pedological horizons, and were sampled discontinuously (ca. 5 cm vertical distance between samples) in order to avoid mixing of samples. From each level 7 to 10 kg of soil was collected. Collecting this large amount of soil is necessary when the bulk of charcoal in the soil is unknown *a priori*, in order to be sure to extract enough charcoal fragments for identification and dating (Thinon, 1992; Carcaillet and Thinon, 1996).

3.2. Charcoal extraction

The soil samples were air dried before sieving to harden the charcoal, which was weakened by the long presence in humid soil. Once dried, the samples were left to soak in ca. 25 l of water for a few hours, this dispersed soil aggregates and made sieving easier. We sieved the soil with running water through a column of two sieves with mesh sizes of 2 and 0.4 mm. A sieve with a 5 mm mesh size, as used in this procedure by Carcaillet and Thinon (1996), was not necessary, because there were no stones present in the soil. The 2 mm sieve retained the largest charcoal fragments, plus organic material, mostly root fragments. The 0.4 mm sieve retained the rest of the charcoal fragments that were large enough for identification, plus the sand fraction of the soil. After drying, the charcoal was manually separated from the sand and the organic material under a dissection microscope.

3.3. Wood sampling and construction of charcoal reference collection

Generally, the identification of soil charcoal fragments is based on comparison with wood anatomy atlases and reference collections of wood (xilotheca) and charcoal (anthracotheca). For the species in our study area, the wood anatomy was unknown (P. Gasson of Kew Royal Botanical Gardens, pers. comm. 2006); for South America the only available references are a wood anatomy atlas for Amazonian species (Détienne and Jacquet, 1983), and some material from specific studies in south eastern Brazil (Scheel-Ybert et al., 1998). We therefore created the reference material for the species of our study area ourselves. To this end we collected wood samples of all woody species that were encountered in our floristic survey (Table 1). Stems or branches (15–20 cm long, min. 10 cm diameter if possible) of five individuals of each species were sampled. Species were identified at the QCA herbarium of the Pontificia Universidad Católica del Ecuador in Quito. Nomenclature (incl. authors and families) is according to Jørgensen et al. (1999).

The wood samples were used to create the xilotheca and the anthracotheca, and a database of anatomical features (Fig. 4; Table 2). The wood samples were observed and described on the three fundamental wood plains (transverse, longitudinal tangential and longitudinal radial) using an electron microscope. The anatomical descriptions were based on the IAWA list of microscopic features for hardwood identification (Wheeler et al., 1989). The procedure was repeated with modern charcoal samples, because the identification is based on comparison directly with charcoal rather than wood. Charcoal was observed using an incident light microscope (100×, 200×, 500× and 1000×). To create charcoal from the wood samples, the air-dried samples were covered by sand to restrict the oxygen supply to avoid total combustion, and heated in a muffle furnace at 350 °C for 20 min (Machado Yanes, 1992). The woody structures of the caulescent fern *Blechnum* were studied, but they were not included in the database, because the database is based on the wood anatomy of angiosperms.

3.4. Charcoal identification

For taxonomical identification, all soil charcoal fragments were observed through an incident light microscope and compared to the reference collections.
Our database did not yet include all the collected species, and some species previously present in the study area may be absent in the modern vegetation. However, to reconstruct treeline position we only needed a few species that could be confidently identified and that could serve as indicators to distinguish forest and páramo.

The selection of indicator species was based primarily on their unique occurrence in either forest or páramo, in combination with their abundance in the actual vegetation, and the identifiability of their wood anatomy. We based the assignment of species to forest or páramo on their distribution in our study area and on information available in the literature (Cleef and Hooghiemstra, 1984; Kuhry, 1988; Gentry, 1995; Mora, 1998; Marchant et al., 2002b) (Table 1). Much of the latter information referred to genera and not to individual species. Also, species of the same genus may have

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**Fig. 4.** Microscopic features of the wood of the indicator species for forest and páramo, from Guandera Biological Station. Selected electron microscope photographs of wood anatomy: a–b *Espeletia pycnophylla*, transverse and radial (wood) section; c–d *Pernetia prostrata*, transverse (wood) and radial (charcoal) section; e–f *Pentacalia vaccinoides*, transverse and radial (charcoal) section. For details see Table 2.
similar wood structures and their charcoal might be confused. Therefore indicator species were preferred that had a strong habitat preference on the genus level. The indicator species for forest were *Ilex colombiana*, *Clusia flaviflora*, *Oreopanax confusus*, and *Ocotea infrafoveolata*. The indicator species for páramo were *Espeletia pycnophylla*, *Pernettya prostrata*, and *Pentacalia vaccinioidea*. The presence of these species in the charcoal record was considered a dominant indication of the vegetation physiognomy at the time of charcoal formation. If we consider that present-day vegetation associations may differ from the associations that existed in the past, the use of indicator taxa may pose some problems. Still, trees and heliophilous shrubs should provide quite good indicators for forest and lower páramo-like vegetation respectively.

### 3.5. Charcoal quantification and dating

The amount of charcoal in the soil was expressed as the soil charcoal concentration (mg charcoal/kg dry soil: ppm), which includes only charcoal particles $\geq 0.4$ mm. This quantity was calculated per level and for the whole profile.

Nine charcoal samples from different pits and levels were radiocarbon ($^{14}$C) dated by accelerator mass spectroscopy (AMS). Where possible, the dating was performed on single identified charcoal fragments (Carcaillet, 2001).
However, to collect the minimum quantity of charcoal necessary for dating (1 mg), it was often necessary to use two or more fragments. Where possible, we used identified charcoal fragments of the same species, but in two cases we used a bulk sample of unidentified charcoal (Table 3). In the organic layer of the forest soil charcoal was absent, so macro remains of roots were dated instead.

As a pre-treatment for AMS dating, each sample was mechanically cleaned with tweezers under a dissection microscope, and chemically cleaned from absorbed mineral carbonates and organic matter with cycles of hydrochloric acid (HCl 3%) and sodium hydroxide (NaOH 3.2%) alternated by neutralization with de-ionized water. For further purification, samples were submitted to a pyrolysis process by heating them in a glass tube with a Bunsen burner for ca. 10 min under nitrogen flow.

Some samples were dated at the Dynamitron Tandem Laboratory in Bochum, Germany (Lubritto et al., 2004). Other samples were dated at the Center for Isotopic Research on Cultural and Environmental Heritage (CIRCE) in Caserta, Italy (Terrasi et al., 2007) (Table 3). All samples were pre-treated at the latter facility, and labeled DSA. The $^{14}$C ages were calibrated with Calib 4.4 (Stuiver et al., 1998), using 1σ probability distributions.

4. Results

4.1. Modern vegetation

The modern vegetation around the upper páramo pit (GUA1) was tussock grass páramo. The tussock grasses (*Festuca* and *Calamagrostis*) had a ground cover of ca. 80% and an average height of 15 cm. *Espeletia pycnophylla* and *Puya hamata* were abundant, and shrubs had a ground cover of only 5% and an average height of 25 cm. Shrub species found were *Loricaria ferruginea*, *Pentacalia vaccinoides*, *Hypericum laricifolium* and *Diplostephium vaccinoides*. There was abundant regeneration of *E. pycnophylla*.

The modern vegetation around the lower páramo pit (GUA2) was also tussock grass páramo. The tussock grasses had a ground cover of ca. 60% and an average height of 35 cm. Compared to GUA1, shrubs had a higher ground cover (15%) and were higher (50 cm), and *H. laricifolium* was more abundant.

The modern vegetation around the forest pit (GUA3) was *Clusia* forest. The 20-m high canopy layer had a cover of ca. 70% and was dominated almost completely by *C. flaviflora*, although *Weinmannia coehensis* also occurred. The sparse lower canopy layer (8–10 m) was composed of *Oreopanax confusus* and *Miconia tinifolia*. Caulescent *Blechnum* ferns (0.5–1.5 m high) covered ca. 15%, and Bromeliaceae dominated the herb layer, which had 40% ground cover, and were abundant as epiphytes. Moss cover was low (15%) compared to mixed forests in the area, and litter cover was high (35%). No tree seedlings or saplings were observed in the plot, and they also appeared to be rare in other parts of the *Clusia*-dominated forest.

### 4.2. Charcoal age and concentration

The age of the charcoal from the deepest soil levels was similar in all pits, at ca. 13,000 cal years BP, corresponding to the Pleistocene–Holocene transition (Table 3). So the profiles represent a sequence for the entire Holocene, although there is a hiatus between ca. 12,500 and 4000 cal BP.

<table>
<thead>
<tr>
<th>Lab. code</th>
<th>Profile — level</th>
<th>Depth (cm)</th>
<th>$^{14}$C year BP</th>
<th>Cal year BP (1σ)</th>
<th>Taxa dated (number of fragments)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DSA345</td>
<td>GUA1 — II</td>
<td>20–40</td>
<td>* 2026±39</td>
<td>2006–1924</td>
<td>Unidentified (3)</td>
</tr>
<tr>
<td>DSA342</td>
<td>GUA1 — IV</td>
<td>60–80</td>
<td># 3692±47</td>
<td>4091–3972</td>
<td><em>Blechnum</em> sp. (7)+ Unid. (5)</td>
</tr>
<tr>
<td>DSA341</td>
<td>GUA1 — V</td>
<td>80–108</td>
<td># 10,596±367</td>
<td>13,033–11,944</td>
<td><em>Pentacalia vaccinoides</em> (1)</td>
</tr>
<tr>
<td>DSA322</td>
<td>GUA2 — IV</td>
<td>75–100</td>
<td># 4364±51</td>
<td>4975–4860</td>
<td><em>Diplostephium</em> sp. (1)</td>
</tr>
<tr>
<td>DSA754</td>
<td>GUA2 — V</td>
<td>100–125</td>
<td># 7236±32</td>
<td>8110–7976</td>
<td><em>Pentacalia vaccinoides</em> (1)</td>
</tr>
<tr>
<td>DSA313</td>
<td>GUA2 — VI</td>
<td>125–150</td>
<td># 10,886±158</td>
<td>13,133–12,823</td>
<td>Unidentified (2)</td>
</tr>
<tr>
<td>DSA312</td>
<td>GUA2 — VII</td>
<td>150–195</td>
<td># 10,964±167</td>
<td>13,158–12,854</td>
<td><em>Pentacalia vaccinoides</em> (7)</td>
</tr>
<tr>
<td>DSA575</td>
<td>GUA3 — III</td>
<td>60–100</td>
<td># modern</td>
<td>12,994–12,825</td>
<td><em>Clusia flaviflora</em>, root (1)</td>
</tr>
<tr>
<td>DSA549</td>
<td>GUA3 — V</td>
<td>120–140</td>
<td>* 5050±30</td>
<td>5889–5807</td>
<td><em>Pernettya prostrata</em> (1)</td>
</tr>
<tr>
<td>DSA551</td>
<td>GUA3 — VII</td>
<td>170–200</td>
<td>* 10,842±46</td>
<td>12,994–12,825</td>
<td><em>Pentacalia vaccinoides</em> (1)</td>
</tr>
</tbody>
</table>

Charcoal was dated by AMS either at the Dynamitron Tandem Laboratory (Bochum Universität, D, #) or at the Center for Isotopic Research on Cultural and Environmental Heritage (Seconda Università di Napoli, I, *). The AMS $^{14}$C measurements were calibrated using the CALIB 4.4 software (Stuiver et al., 1998).
years BP in GUA1 (Fig. 5). Charcoal ages decreased with decreasing depth in the soil, with no inversions of charcoal age with depth, indicating an ordered stratification of the charcoal in the soil (Fig. 5).

Charcoal was present at all depths in all soil profiles, except in the organic layer in the forest (levels I, II and III of GUA3) (Fig. 6). The charcoal concentration was highest at 125–150 cm in the lower páramo (level VI, GUA2), corresponding to ca. 13,000 cal years BP. A second peak is seen in the higher páramo at 25–50 cm (level II, GUA1), corresponding to ca. 2000 cal years BP. Very little charcoal was present in the organic soil immediately underlying the organic layer in the forest (level IV, GUA3).

4.3. Charcoal identities

Identification of soil charcoal fragments was possible to the genus level, and often even to the species level (Fig. 6). Páramo indicator taxa were found in all profiles.
from ca. 13,000 cal years BP until present (in the páramo, GUA1 and GUA2) or until ca. 5850 cal years BP (in the forest, GUA3). No forest indicator taxa were found in any charcoal sample. Several taxa were found that, in combination with the páramo indicator taxa, may indicate the presence of a shrubby páramo or subpáramo type vegetation (*Diplostephium*, *Miconia*). The uppermost level (level I) of both páramo profiles contained charcoal of *Espeletia*, a species now very abundant in the tussock grass páramo.

![Soil profiles from the páramo (GUA1 and GUA2) and from the forest (GUA3) in Guandera Biological Station, northern Ecuador. The black bars represent the charcoal concentration per level expressed as mg(charcoal) kg$^{-1}$(dry soil). Dates are expressed in calibrated years BP. Taxa of identified charcoal are reported for each level.](image-url)
5. Discussion

The presence of páramo taxa throughout all three soil profiles, especially in combination with the absence of forest taxa, shows that the treeline in the study area has moved up to its present position only very late in the Holocene (after ca. 5850 cal years BP). A treeline ecotone or sub-páramo may have reached up to 3810 m asl after ca. 4900 cal years BP. The presence of charcoal throughout the profiles also shows that fires have occurred in this area at least since the Pleistocene–Holocene transition ca. 13,000 cal years BP. These fires have not turned forest into páramo, but they have possibly prevented forest extension into the páramo.

The presence of Pentacalia charcoal in the deepest level of each profile, aged ca. 13,000 cal years BP, confirms the findings of Hooghiemstra and Cleef (pers. comm. 2006), who interpret abundant Pentacalia pollen in samples of the same age in combination with abundant grass pollen as a grass páramo interspersed with patches of Pentacalia shrubs. It is not surprising that we find this type of cold-climate vegetation in the coldest period of the El Abra stadial (Van’t Veer et al., 2000). However, at ca. 5850 cal years BP there was still páramo vegetation even at the lowest sampling point, where we now find forest (level V of GUA3, at 3540 m asl). This is evidenced by the presence of charcoal from Pernettya prostrata, which is a typical tussock grass páramo species (Kuhry, 1988), plus the absence of charcoal from forest species. This is in contradiction with palynological studies from Colombia and Ecuador which show a rise of the treeline to its present altitude already at the beginning of the Holocene (Van Der Hammen, 1974; Flenley, 1979).

After ca. 5850 cal years BP there is only very little charcoal present in the forest profile (GUA3, at 3540 m asl), which may indicate that fires were less frequent. The absence of fires apparently allowed the actual forest to develop, while in turn the moisture of the forest would have suppressed further fires. So the actual forest is certainly < 5000 years old (the age of level V) and could be < 4000 years old (the extrapolated age of level IV). The dating of the lowest layer of organic forest soil revealed an age of 100 14C years. However, the dated material was a root — most of the organic layer consists of roots — and we cannot exclude that this root has penetrated this deepest level long after forest formation. Considering the large size of the Clusia trees, the forest must certainly be well over 100 years old. Moreover, observations on the floristic composition and structure of the Clusia forest suggest that this is a late-successional forest type. The time of first forest establishment may therefore be even much earlier than the age of the actual Clusia forest would suggest.

At the highest altitude (GUA1, at 3890 m asl), páramo taxa were present throughout the profile, so we conclude that at this altitude there has been páramo vegetation during the entire Holocene, even if the hiatus between 12,500 and 4000 cal years BP do not allow for very definite conclusions based on this profile alone.

In the middle pit (GUA2, at 3810 m asl), some species are present from ca. 8000 cal years BP (level V) that indicate a more shrubby vegetation, possibly similar to some contemporary sub-páramo shrub types. This shrubby vegetation lasted until at least to ca. 4900 cal years BP, but due to a lack of identifiable charcoal and a lack of datings, it is not yet possible to deduce when tussock grass reached a dominance equivalent to that seen today. The presence of a páramo indicator (Pentacalia) shows that there was no closed forest at 3810 m. However, the presence of the genera Miconia and Diplostephium, which comprise shrubs characteristic for treeline ecotones (Marchant et al., 2002b) and for dwarf forest and dwarf shrub páramo (Cleef and Hooghiemstra, 1984), may indicate that the treeline was situated not far below this altitude, although the site may also have been part of an extensive zone of shrub-páramo. If the treeline ever rose above its present altitude at 3600 m asl, this must have happened only after ca. 5850 cal years BP, as forest did not establish before this time at 3540 m. Whether the treeline has really been higher than the present 3600 m asl in the late Holocene remains to be investigated with additional sampling points closer to the treeline.

The increased importance of shrubs during the middle Holocene indicates a relatively moist or warm climate, perhaps combined with a decreased fire frequency as a result of increased moisture or decreased land use. Warmer conditions favorable for forest growth were also suggested for the middle Holocene in Colombia by Van Der Hammen (1974), who states that treelines moved up to above their present position during this ‘hypothermal’ period. Other palynological studies in Colombia found depressed treelines during this period, which they attribute to a drier climate (Marchant et al., 2001). The increase in forest pollen that Van Der Hammen (1974) found, has also been interpreted as a decline in páramo flora (leading to an overrepresentation of long-distance forest pollen), suggesting a dryer or colder climate (Markgraf, 1989; Horn, 1993). The original interpretation appears to be supported by δ18O data from Peruvian glaciers, which indicate a warm period from 8400 to 5200 14C years BP (Thompson et al., 1995). The higher temperatures would
have caused a rise of the treeline where temperature was limiting, while at the same time, if this period was also drier, this would have caused a lowering of the treeline where moisture was locally limiting. This may explain part of the contradictions in different treeline reconstructions for this period. Still, the contrasting conclusions that can be drawn from the same data (Van Der Hammen, 1974; Markgraf, 1989) also show the inherent uncertainty in palynological interpretations.

The presence of charcoal from ca. 13,000 cal years BP indicates that fires have been part of this ecosystem for a long time. However, we did not find indications that fire has destroyed forests and thus created páramo. Rather, fires may have inhibited or slowed down forest expansion, possibly together with other inhibiting factors such as excess solar radiation and extreme daily temperature fluctuations in the páramo (Bader et al., 2007a). Similarly, Horn (1993) concluded that although fires had occurred during all of the Holocene in a Costa Rican páramo area, ‘these fires have not carved páramo from forest.’ This is in contrast with the view that forest patches in the páramo are remnants of formerly more extensive forests (Ellenberg, 1958; Laegaard, 1992; Sarmiento and Frolich, 2002).

Regarding the uncertain status of forest patches above the treeline, the most likely hypothesis offered so far is that the highest of these patches are restricted to favorable microsites, while the lower patches may be remnants of formerly more extensive zonal forests (Miehe and Miehe, 1994; Kessler, 2002; Wille et al., 2002). However, based on our results it appears more likely that many patches are neither remnants nor extrazonal islands, but foreposts of an expanding forest that has been stopped by frequent páramo fires. Both the special microclimatic or edaphic conditions and the protection from fire that are typical of the common locations of forest patches (boulder slopes, ravines, topographical hollows) would contribute to such a scenario: trees may establish earlier and grow faster in such locations, and because of their size be less susceptible to fire, and by competition reduce the biomass (= fuel load) of surrounding tussock grasses. If, on top of that, the fire frequency or the fire intensity is lower because of a protected position, forest patches can develop while the surrounding areas remain páramo.

At present, natural fires are unlikely to occur because regular thunderstorms keep the vegetation wet and there are few sources of natural ignition, e.g. active volcanoes. However, during the early Holocene, as well as several later periods, the Andean climate appears to have been drier than today (Van’t Veer et al., 2000; Marchant et al., 2001, 2002b; Vélez et al., 2003), this may have resulted in a higher frequency of natural fires. For the Andes, the presence of charcoal at the Pleistocene–Holocene transition is generally explained by this drier climate, and this type of interpretation is applied until the middle Holocene. Only when the first direct evidence of anthropogenic disturbance is found in the pollen record (pollen from agricultural and disturbance species), are fires generally attributed to man (Hansen and Rodbell, 1995; Marchant et al., 2001; Wille et al., 2002; Hansen et al., 2003; Bush et al., 2005).

The first appearance of humans in South America is dated at the Pleistocene–Holocene transition (Fiedel, 1999; Gnecco, 2003). These first inhabitants did not practice agriculture, so no pollen of disturbance vegetation or agricultural species witness their presence, but they could leave traces of fire (Piperno et al., 1990). They were hunter-gatherers and, just like is still happening on the mountains of East-Africa (Wesche et al., 2000), mountain grasslands or shrublands may have been burned to facilitate hunting. Also, fires may reflect the use of the areas with open vegetation above the treeline for traveling (Hermes, 1955). In this way early human populations may have already influenced the high-altitude vegetation in the beginning of the Holocene, possibly preventing forest expansion into the páramo. However, the distinction between natural and anthropogenic fires can not be made, so we are restricted to speculations as to the origin of the palaeofires, and hence as to the ‘naturalness’ (as opposed to man-made origin) of the lower parts of the modern páramo.

Charcoal particles \( \geq 0.4 \ mm \) provide information about local fires (Patterson et al., 1987; Ohlson and Tryterud, 2000). The charcoal concentration found in the soil depends on the type and quantity of the burned biomass (Carcaillet, 1998) and on the time since burning (Di Pasquale, 1998). This concentration is therefore not a simple measure for the fire frequency. Still, the strong correspondence in the timing of the charcoal peak in level VI of GUA2 and that found on a continental scale by Haberle and Ledru (2001) may indicate an increased fire frequency during this period, and asks for further investigation.

The pedoanthracological methods used here have some clear advantages over the more traditional palynological methods, most importantly the high spatial resolution that can be obtained thanks to the local nature of the charcoal proxy. A disadvantage is the large amount of soil needed to extract sufficient identifiable charcoal, which implies that the levels from which soil is collected are relatively thick, resulting in a low temporal resolution. This coarse sampling may partly explain the hiatuses in our chronologies, but these discontinuities...
may also be due to erosion. The origin of the hiatuses will be addressed in further analysis of the soil profile.

Soil charcoal data from a small number of pits is sufficient to provoke many interesting hypotheses about vegetation history, and falsify others. Still, a more detailed spatial analysis of past vegetation cover requires a larger number of sampling points. Considerable improvement can also be made by the extension of the charcoal reference collection, which is in fact being extended continuously. Based on the results described here, additional sampling points were located at optimal positions for detailing the speed and timing of treeline movements. Data from these additional profiles are being investigated at present.

6. Conclusions

The charcoal records in the studied soils represent the entire Holocene, starting at ca. 13,000 cal years BP. The presence of páramo taxa throughout all three records, especially in combination with the absence of forest taxa, shows that the treeline in the study area has moved up to its present position only recently (after ca. 5850 cal years BP). During the middle Holocene (7200–4400 14C years BP) there was a period favorable for shrub and tree growth, and the treeline may have risen most during this period. However, the treeline has never reached 3890 m asl, and we have no strong indication that it ever reached 3810 m asl. The presence of charcoal throughout the profiles also shows that fires have occurred in this area at least since the beginning of the Holocene. These fires have not caused a downward movement of the treeline, but they have possibly slowed down forest extension into the páramo. Further research will focus on detailing the speed and timing of treeline rise.

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References


